FIRST RECORD OF *CAENOCHOLAX FENYESI* (STREPSIPTERA: MYRMECOLACIDAE) PARASITIZING *SOLENOPSIS INVICTA* (HYMENOPTERA: FORMICIDAE) IN ARGENTINA, WITH A DISCUSSION ON ITS DISTRIBUTION AND HOST RANGE[1]

Jerry L. Cook[2], Luis A. Calcaterra[3], and Lucas Nuñez[4]

ABSTRACT: The first record of *Caenocholax fenyesi* parasitizing the red imported fire ant, *Solenopsis invicta,* in South America is documented. *Caenocholax fenyesi* males were collected from colonies of *S. invicta* in northeastern Argentina. This record helps to clarify the occurrence and host utilization of *C. fenyesi* in the United States, where *S. invicta* is an invasive exotic species. This record, along with other recent reports, suggests that *C. fenyesi* males are generalist parasites, not utilizing a narrow host range, as do most known strepsipterans. However, the potential presence of cryptic species is an alternate explanation.

KEY WORDS: *Solenopsis invicta, Caenocholax fenyesi,* host association, distribution, host specificity, host switching

Host relationships in the strepsipteran family Myrmecolacidae are poorly known. However, in all species whose host has been documented, a form of heteronomy exists (Kathirithamby 1989). Males utilize ants (Hymenoptera, Formicidae) as hosts during their developmental stages, while females use orthopteroids for developmental stages and as the host of adult females (Kathirithamby and Hamilton 1992). Most species of Myrmecolacidae are known only from males, which are collected in their adult, free-living stage. These adult males are rarely collected with a host association, and hosts are currently known for males of eight of the 108 myrmecolacid species (Westwood 1861, Hofeneder 1949, Luna de Carvalho, 1972, 1973, Tesón & Remes Lenicov 1979, Kathirithamby 1991, and Kathirithamby and Johnston 1992, 2003). Additionally, several parasitized ant species have been collected but their associated strepsipteran species was not identified (Ogloblin 1939, Hughes et al. 2003).

The first host association between *Caenocholax fenyesi* Pierce and the red imported fire ant, *Solenopsis invicta* Buren, was discovered by Kathirithamby and Johnston (1992) in Texas, USA. This host association was considered as a crossover host since it appeared unlikely that parasitized *S. invicta* and the unknown orthopteroid female host were both simultaneously introduced and

[1] Received on March 31, 2004. Accepted on July 16, 2004.

[2] Department of Biological Sciences, Sam Houston State University, Huntsville, Texas 77341-2116 U.S.A. E-mail: bio_jlc@shsu.edu.

[3] USDA-ARS South American Biological Control Laboratory, Bolivar 1559 Hurlingham, Buenos Aires Province, Argentina. E-mail: trapisonda@tutopia.com.

[4] USDA-ARS South American Biological Control Laboratory, Bolivar 1559 Hurlingham, Buenos Aires Province, Argentina.

migrated throughout the southeastern United States in a span of less than 75 years (Cook 1996). Kathirithamby and Hughes (2002) discovered *Camponotus planatus* Roger parasitized by *C. fenyesi* in Veracruz, Mexico, and speculated that *C. planatus* was the original host of *C. fenyesi.* This discovery was from the vicinity of the type locality of *C. fenyesi* (Pierce 1909). *Dolichoderus bispinosus* Olivier was also recently found hosting *C. fenyesi* in the same Mexican locality (Hughes et al. 2003). Genetic studies by Kathirithamby and Johnston (2003) report that male *C. fenyesi* from Texas in *S. invicta* are 15 percent divergent from the morphologically identical male from Mexico, parasitic in *D. bispinosus.* This led them to name *C. fenyesi* from Texas *C. fenyesi texensis* and from Mexico *C. fenyesi waloffi.*

The first report of *Caenocholax* in South America was given by Ogloblin (1939) from collections in Argentina and Brazil. Ogloblin found male specimens in *Pheidole radoschkowski reflexans* Santschi that he reported as a new species of *Caenocholax,* but did not name the strepsipteran species. He found more of this strepsipteran species in *Pheidole fallax emiliae* Forel and an additional undetermined *Pheidole* species. Ogloblin also found three fire ant species; *Solenopsis saevissima pylades* Forel (now *S. xyloni*), *S. saevissima quinquecuspsis* Forel (now *S. quinquecuspis*), and *S. saevissima richteri* Forel (now *S. richteri*) in Missiones and Salta province, Argentina, that he reported as being parasitized by an undetermined species of *Myrmecolax.* This species was named *Myrmecolax ogloblini* by Luna de Carvalho (1973). Later, Tesón and Remes Lenicov (1979) observed specimens from the Ogloblin collection taken from the *Pheidole* species (labeled as *Caenocholax pheidolephagus,* but never published) and determined that they were *Caenocholax brasiliensis* Oliveira and Kogan. *Caenocholax brasiliensis* and *M. ogloblini* have since been synonymized with *C. fenyesi* (Kathirithamby and Hughes 2002).

The distribution of *C. fenyesi* confirms that its males must be hosted by more than one ant species, unless *C. fenyesi* constitutes a species complex. *Caenocholax fenyesi* has a currently known range from the southern United States to Chile and Argentina (Cook et al. 1997; Kathirithamby and Hughes 2002). While its known distribution now appears disjunct, it is probably widespread throughout this region. New collections continue to fill areas missing from the known distribution. The distribution of *S. invicta* is well known, and it is not found in Mexico, Central America, or Ecuador, where *C. fenyesi* occurs. *Camponotus planatus* is a widely distributed species, but its northern limit includes only the southernmost part of Texas and parts of Florida. Its southern distribution limit does not include Chile and Argentina (W. P. MacKay unpublished data). In this paper we make the first report of *C. fenyesi* parasitizing *S. invicta* in its homeland and discuss its host relationships.

NEW HOST ASSOCIATION RECORDS

Fifteen *Caenocholax fenyesi* males were isolated from four *Solenopsis invicta* colonies from northeastern Argentina. The *S. invicta* colonies were being maintained in laboratory rearing conditions at USDA-ARS-SABCL as part of a study of preference of *Pseudacteon* flies (Diptera: Phoridae) for different fire ant hosts. Two colonies were collected on September 11, and the others on November 20, 2003. Three colonies were from Herradura (S 26° 31', W 58° 17'), Formosa Province, on

the coast of the Paraguay River. The other colony was collected near Centro Nacional de Desarrollo Acuícola (CENADAC), 20 km from Corrientes (S 27° 23', W 58° 41'), Corrientes Province, on the coast of the Paraná River. Both collecting sites are located in the eastern limit of the phytogeographical province of the Chaco. This province has a mean annual temperature of 20 to 23°C and an annual rainfall of 1,200 mm (Cabrera and Willink 1980) with a pronounced dry season. The area where the colonies were collected has a somewhat higher rainfall because it is located near a tropical rain forest habitat and the main rivers of the region (Paraná and Paraguay).

Colonies were collected, separated from the soil by flotation (Banks et al. 1981), and housed in ventilated plastic rearing trays (40 x 30 x 15 cm) with plastic cover and a 7-cm plaster nest to provide humidity. Trays containing 2g of worker ants (~3000 ants) and 2g of brood were maintained at 25°C and 60 percent RH, fed sugar water, and provided water *ad libitum.* The trays were being examined daily for the presence of *Pseudacteon* (Phoridae) pupae. *Caenocholax fenyesi* males were found between October 3 and 20, 2003, with additional specimens collected between December 19, 2003, and January 2, 2004.

We found only 15 *C. fenyesi* males from the approximately 12,000 *S. invicta* workers. Supposing the males emerged from different workers as is typical for this species (Cook 1996), the parasitism rate from these colonies was less than 0.2 percent. However, this may be an underestimation because stylopized ants lose their social instincts and abandon the nest (Ogloblin 1939, Cook 1996).

The strepsipterans were morphologically identified in the laboratory at Sam Houston State University. Three male *C. fenyesi* from this collection are deposited in the entomology collection at Sam Houston State University. The other individuals were kept at the SABCL collection.

In addition, a survey was conducted to search for *C. fenyesi* females in late November and early December 2003 in both areas where the *S. invicta* colonies were found parasitized. A total of 217 orthopterans were collected and examined, but none were parasitized by *C. fenyesi.* Collecting methods were light trapping (three hours each day and for three days), sweeping (during 30 minutes), and pitfall trapping (40 vials were put every 10 m for two days). In Herradura, 154 orthopterans (70 Grillidae, 77 Acrididae, and 7 Gryllotalpidae) were collected in the light traps and 8 Grillidae in the pitfall traps (2 of them were parasitized with dipteran parasites). In Corrientes, 35 orthopterans were collected from sweeping (1 of them parasitized by a nematode).

DISCUSSION

The lack of information on host associations in the Myrmecolacidae is common, and in the case of *C. fenyesi* has led to several speculations about its host relationships. Cook (1996) speculated that *C. fenyesi* most likely did not move with its host from *S. invicta's* introduction into Mobile, Alabama, around 1918 (Creighton 1930) to Texas by its discovery in 1988 (reported by Kathirithamby and Johnston 1992). This move would have required a simultaneous move of both sexes, which occur in different hosts, or by the first larval instar. The dispersal stage is the first instar

larva, which must find and infect its host. It is unlikely that a 50μ larva, which moves by walking legs and sometimes jumping with its caudal appendage, will disperse very far in any given generation (Cook et al. 1998). Although dispersal may also be mediated by a host female, which may disperse into an area where suitable hosts for both strepsipteran hosts occurs.

Kathirithamby and Hughes' (2002) discovery of *C. fenyesi* using *C. planatus* as a host led them to speculate that it may be the original host. This supposition presents two problems, how *S. invicta* became its host in central Texas and why *C. planatus* would be the most likely original host. First, if *C. fenyesi* made a host switch from *C. planatus* to *S. invicta*, there is a logistical problem. *Camponotus planatus* only occurs in Texas in southern counties of the Rio Grande Valley, and the closest it has been reported to Brazos County (location of the material for the original host association) is the material that we (JLC) collected in San Patricio County and separate material collected by William P. Mackay from Victoria County (O'Keefe et al. 2000). *Solenopsis invicta* did not invade this region of Texas until the mid-1970s (Callcott and Collins 1996). The original host association that Kathirithamby and Johnston (1992) described was from specimens collected in 1988. While it is not impossible that *C. fenyesi* dispersed this far, it is unlikely given the dual host association of this strepsipteran and its low dispersal ability. It is even more unlikely that *C. planatus* is the source of *C. fenyesi* collected in Louisiana between 1964 and 1967 (Khalaf 1968), in Mississippi in 1966 (Khalaf 1969), and in 1960 from Arizona (Johnson and Morrison 1979). The presence of *C. fenyesi* in Arizona is most problematic to support the speculation of Kathirithamby and Hughes because neither *C. planatus* nor *S. invicta* are known to occur in Arizona. The second problem of what ant species is the original host of *C. fenyesi* is becoming more difficult to determine with the discovery of different host associations. The host record of *C. planatus* from the type locality of *C. fenyesi* does not necessarily suggest that it is the original host, but only documents that this could be the host of the type population. More recently, *D. bispinosus* has also been recorded from this region in Mexico, making even that assumption unclear.

The discovery of *C. fenyesi* utilizing *S. invicta* as a host in its native Argentina makes it an additional candidate as a primary host. The recent discovery of *S. invicta* in northwestern Argentina (Calcaterra et al. unpublished data), where males of *C. fenyesi* were also collected (Kathirithamby and Hughes 2002), could support this idea. All of these host ants are being parasitized in their natural habitats, as well as *S. invicta* being parasitized in its invaded territory of the United States. None of these ant species are found throughout the range of *C. fenyesi,* so there is a problem with designating any of them as an "original host," at least from the evidence that we now have. Other likely candidates could be other fire ants with wide distributions, such as *Solenopsis xyloni* McCook or *Solenopsis geminata* Fabricius, however, there is no concrete evidence that either is even a host. The only evidence for this assumption is that their distributions coincide in part with that of *C. fenyesi;* they are closely related to one known host, *S. invicta;* and Ogloblin's (1939) discovery of a specimen of what he identified as *S. s. pylades* Forel parasitized by a myrmecolacid that he did not identify. *Solenopsis saevissima pylades* is now a synonym of *S. xyloni* (Trager 1991). However, the identity of this *Solenopsis* species

needs confirmation because *S. xyloni* is not thought to occur in South America (Trager 1991, Pitts 2002). The host found in Misiones by Ogloblin could be *S. invicta, S. richteri,* or *S. macdonaghi. Solenopsis invicta* is the most abundant of these species in this area.

One conclusion that can now be garnered from the data we have is that male *C. fenyesi* is a generalist parasite of ants. If all of these strepsipteran specimens belong to the same species, *C. fenyesi,* then it certainly is not host specific. Males of *C. fenyesi* are currently associated with three species of ants that are not even in the same subfamily (*S. invicta* is in the subfamily Myrmicinae, *D. bispinosus* in Dolichoderinae, and *C. planatus* in Formicinae). The female would also be a generalist with our current associations. One host of the female *C. fenyesi* has been identified by Kathirithamby and Johnston (2003) as the cricket *Macroanaxipha macilenta* (Saussure). Prior to this, Kathirithamby and Hughes (2002) synonymized *Myrmecolax ogloblini* Luna de Carvalho under *C. fenyesi,* which would be an additional host for the female. Myrmecolax ogloblini was described from material Ogloblin had collected and called *Mantidoxenos argentinum.* The hosts of this species are *Camponotus punctulatus cruentatus* Forel for the male and *Acanthiotespis maculaus* (Saussure) for the female (Luna de Carvalho 1973). *Acanthiotespis maculatus* is in the order Mantodea. If this synonymy is correct it would mean that the female is utilizing hosts in at least two separate orders, Mantodea and Orthoptera.

An alternate conclusion may be that there are cryptic species that are all morphologically similar to *C. fenyesi.* In this scenario, different host species may have different strepsipteran parasites. In the light of Kathirithamby and Johnston's (2002) genetic analysis, this may be more logical. Molecular approaches and host specificity tests are needed to clarify this subject.

ACKNOWLEDGEMENTS

We thank Sanford Porter (USDA-ARS-Center for Medical, Agricultural, and Veterinary Entomology) and Juan Briano (USDA-ARS-South American Biological Control Laboratory) for reviewing the manuscript.

LITERATURE CITED

Banks, W. A., C. L. Lofgren, D. P. Jouvenaz, C. E. Stringer, P. M. Bishop, D. F. Williams, D. P. Wojcik, and B. M. Glancy. 1981. Techniques for collecting, rearing, and handling red imported fire ants. United States Department of Agriculture, Advances in Agricultural Technology, Southern Series 21: 1-9.

Cabrera, A. L. and A. Willink. 1980. Biogeografia de América Latina. OEA, Serie Biológica 13. Washington, District of Columbia, U.S.A. 122 pp.

Callcott, M. A. and H. L. Collins. 1996. Invasion and range expansion of imported fire ants (Hymenoptera: Formicidae) in North America from 1918-1995. Florida Entomologist 79: 240-251.

Cook, J. L. 1996. A study of the relationship between *Caenocholax fenyesi* Pierce (Strepsiptera, Myrmecolacidae) and the red imported fire ant, *Solenopsis invicta* Buren (Hymenoptera, Formicidae). Ph.D. Dissertation (Entomology) Texas A&M University, College Station, Texas, U.S.A. 172 pp.

Cook, J. L., J. S. Johnston, R. E. Gold, and S. B. Vinson. 1997. Distribution of *Caenocholax fenyesi* (Strepsiptera: Myrmecolacidae) and the habitats most likely to contain its stylopized host, *Solenopsis invicta* (Hymenoptera: Formicidae). Environmental Entomology 26: 1258-1262.

Cook, J. L., S. B. Vinson, and R. E. Gold. 1998. Developmental stages of *Caenocholax fenyesi* Pierce (Strepsiptera: Myrmecolacidae): descriptions and significance to the higher taxonomy of Strepsiptera. International Journal of Insect Morphology and Embryology 27: 21-26.

Creighton, W. S. 1930. The new world species of the genus *Solenopsis* (Hymenoptera: Formicidae). Proceedings of the American Academy of Arts and Science 66: 39-151.

Hofeneder, K. 1949. Über einige Strepsipteren. Broteria 18: 109-122, 145-166.

Hughes, D. P., G. Moya-Raygoza, and J. Kathirithamby. 2003. The first record among Dolichoderinae (Formicidae) of parasitism by Strepsiptera. Insectes Sociaux 50: 148-150.

Johnson, V. and W. P. Morrison. 1979. New North American distribution records for four species of Strepsiptera. Entomological News 90: 251-255.

Kathirithamby, J. 1989. Review of the order Strepsiptera. Systematic Entomology 14: 41-92.

Kathirithamby, J. 1991. *Stichotrema robertsoni* spec. n. (Strepsiptera: Myrmecolacidae): the first report of stylopisation in minor workers of an ant (*Pheidole* sp.: Hymenoptera: Formicidae). Journal of the Entomological Society of South Africa 54: 9-15.

Kathirithamby, J. and W. D. Hamilton. 1992. More covert sex: the elusive females of Myrmecolacidae. Trends in Ecology and Evolution 7: 349-351.

Kathirithamby, J. and D. P. Hughes. 2002. *Caenocholax fenyesi* (Strepsiptera: Myrmecolacidae) parasitic in *Camponotus planatus* (Hymenoptera: Formicidae) in Mexico: Is this the original host? Annals of the Entomological Society of America 95: 558-563.

Kathirithamby, J. and J. S. Johnston. 1992. Stylopization of *Solenopsis invicta* (Hymenoptera: Formicidae) by *Caenocholax fenyesi* (Strepsiptera: Myrmecolacidae) in Texas. Annals of the Entomological Society of America 85: 293-297.

Kathirithamby, J. and J. S. Johnston. 2003. The discovery after 94 years of the elusive female of a myrmecolacid (Strepsiptera), and the cryptic species of *Caenocholax fenyesi* Pierce sensu lato. Proceedings of the Royal Society London, B (Suppl.), Biological Letters. Published online 17 Sept. 2003. (DOI 10.1098/rsbl.2003.0078).

Khalaf, K. T. 1968. The seasonal incidence of free Strepsiptera (Insecta) males in southern Louisiana. American Midland Naturalist 80: 565-568.

Khalaf, K. T. 1969. Strepsiptera from the Mississippi Coast. Florida Entomologist 52: 53.

Luna de Carvalho, E. 1972. Quarta contribuicão para o estudo dos Estrepsipteros angolenses (Insecta Strepsiptera). Publicacoes Culturais da Companhia de Diamantes da Angola (Lisbon) 84: 109-130.

Luna de Carvalho, E. 1973. Estudo sobre o *"Mantidoxenos argentinus" (Myrmecolax Ogloblin),* nom. nov. (Insecta Strepsiptera Myrmecolacidae). Ciência Biológica (Portugal) 1: 51-56.

Ogloblin, A. A. 1939. The Strepsiptera parasites of ants. International Congress of Entomology, Berlin 1938 2: 1277-1284.

O'Keefe, S. T., J. L. Cook, T. Dudek, D. F. Wunneburger, M. D. Guzman, R. N. Coulson, and S. B. Vinson. 2000. The distribution of Texas Ants. Southwestern Entomologist 22 (Supplement): 1-92.

Pierce, W. D. 1909. A monographic revision of the twisted winged insects comprising the order Strepsiptera Kirby. Bulletin of the U. S. National Museum 66: 1-232.

Pitts, J. P. 2002. A cladistic analysis of *Solenopsis saevissima* species-group (Hymenoptera: Formicidae). Ph.D. Dissertation (Entomology). University of Georgia. Athens, Georgia, U.S.A. 266 pp.

Tesón, A. and A. M. M. Remes Lenicov. 1979. Estrepsipteros parasitoides de Himenópteros (Insecta – Strepsiptera). Revista de la Sociedad Entomologica. 38: 115-122.

Trager, J. C. 1991. A revision of the fire ants, *Solenopsis geminata* group. Journal of the New York Entomological Society 99: 141-198.

Westwood, J. O. 1861. Notice on the occurrence of a strepsipterous insect parasitic on ants discovered in Ceylon y Herr Niener. Transactions of the Entomological Society of London 5: 418-420.